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SHORT COMMUNICATION

Spiral and web asymmetry in the orb webs of *Araneus diadematus* (Araneae: Araneidae)

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Abstract. Most orb webs are vertically asymmetric with the hub above the geometric center, even though the basic structure of orb webs with concentric sticky spiral loops implies a round shape with the hub in its geometric center. Spiders are known to modify the basic, round web structure to achieve asymmetric webs by placing the sticky spiral loops eccentrically around the hub and by inserting partial sticky spiral loops below the hub. In addition, spiders could increase asymmetry with larger spiral spacing below the hub than above. In the present paper, I analyzed these web modifications quantitatively in webs of *Araneus diadematus* Clerck 1757. In addition, I assessed the influence of gravity on the different web modifications during web building by laying some webs horizontally during auxiliary and/or sticky spiral building, and I also assessed how the web modifications affected each other during web building. I found that web orientation during auxiliary spiral building influenced auxiliary spiral eccentricity, which in turn had an impact on sticky spiral eccentricity and overall web asymmetry. Web orientation, together with web asymmetry and spiral ratio, during sticky spiral building only influenced spiral spacing asymmetry. I conclude that *A. diadematus* uses the auxiliary spiral as a guiding line during sticky spiral building and that it applies different rules to build the two spirals.

Keywords: Gravity, hub displacement, up-down asymmetry, web architecture, web building

Most araneoid orb-web spiders build vertically asymmetric webs, in which the capture area below the hub is larger than the capture area above the hub (e.g., Mayer 1952; Witt & Reed 1965; Risch 1977; ap Rhisiart & Vollrath 1994). Empirical and theoretical studies suggest that this vertical asymmetry is mainly an adaptation to the spider's prey capture behavior, and that it reflects the spider's ability to run downwards faster than upwards (Masters & Moffat 1983; ap Rhisiart & Vollrath 1994; Coslovsky & Zschokke 2009; Maciejewski 2010; Nakata & Zschokke 2010; Zschokke & Nakata 2010). Even though the vertical asymmetry probably has this common cause in all orb webs, the degree of asymmetry varies greatly between and within species (e.g., Witt & Reed 1965; Risch 1977; Heiling & Herberstein 1998; Bleher 2000; Kuntner et al. 2008).

The basic structure of orb webs consists of radial threads that converge at a central point (= hub; Zschokke 1999), around which a sticky thread is placed in concentric spiral loops, forming the capture area (Zschokke 2002). Such a basic web structure implies a round capture area with the hub in its geometric center, as it is indeed found in the ancestral horizontal cribellate orb webs (Wiehle 1927). However, as stated above, the more common vertical ecribellate orb webs, which are the focus of the present study, show a vertical asymmetry. Consequently, in these webs there must be modifications to the basic, round web structure that lead to the observed asymmetry.

The modifications to the basic round web that spiders are known to employ include asymmetrically placed (eccentric) sticky spiral loops (Mayer 1952; Witt & Reed 1965) as well as partial sticky spiral loops below the hub (Reed et al. 1965; Witt & Reed 1965; ap Rhisiart & Vollrath 1994). In addition, spiders could build webs with larger average spiral spacing below rather than above the hub to obtain asymmetric webs. Until this study, it was unclear to what extent spiders employ these modifications in their orb webs.

All orb web spiders build their webs in the same ordered steps (Wiehle 1929; Coddington 1986). After completing the frame and the radii, the spider builds the widely meshed, non-sticky auxiliary spiral starting near the hub and then proceeds outwards. In the *A. diadematus* web, the auxiliary spiral usually has no U-turns (Zschokke 1993). After completing the auxiliary spiral, the spider turns around and starts building the sticky spiral from the periphery inwards. In the *A. diadematus* web, the sticky spiral usually contains several U-turns, most of them at the web's periphery (Mayer 1952; Zschokke 1993). These U-turns lead to partial sticky spiral loops, in most cases in the web's lower part (Fig. 1).

As most orb-web spiders lack acute vision (Land 1985), they must follow non-visual cues during web building. These cues include gravity and the position of earlier laid threads in its vicinity (Peters 1937; Peters 1939; Reed et al. 1965; Witt et al. 1968; Krink & Vollrath 1997). Gravity influences the geometry of the spirals (Vollrath 1986, 1988a). In particular, when there are no gravitational forces parallel to the web plane during web building, spiders build round webs (Mayer 1952; Witt et al. 1977; Zschokke 1993). In addition, the position of threads laid earlier during web building can influence the position of threads built later (König 1951). As an example, coiling and shape of the auxiliary spiral in *A. diadematus* strongly influence coiling and shape of the sticky spiral (Zschokke 1993).

In the present study, I describe the modifications to the basic round web in the webs of *A. diadematus* in detail and assess their contributions to web asymmetry. In addition, I consider the influence of gravity on the different web modifications and on web asymmetry, and describe the relationships among these modifications during web building, (i.e., how do these modifications influence each other?)

METHODS

Second year juvenile and sub-adult *A. diadematus* (males and females) were kept under laboratory conditions (14:10 h L:D, 24± 2° C, 45–55% RH) in Plexiglass frames (30 × 30 × 5 cm). The webs generally had a normal (vertical) orientation during web building, but in order to determine the effects of web orientation (vertical vs. horizontal) during web building, I laid some of these webs horizontally during various phases of spiral building: (i) auxiliary spiral only ($n = 8$), (ii) sticky spiral only ($n = 5$), or (iii) both auxiliary and sticky spirals ($n = 9$). These webs were compared to control webs ($n = 31$) that had a vertical orientation throughout web building.

The completed webs were photographed against a dark background (Zschokke & Herberstein 2005) and the x, y coordinates of the positions of all spiral attachments to one radius at each side of the web (top, left, bottom and right) were entered into the computer with a digitizing tablet for further analysis. The coordinates of entire loops

Figure 1.—Auxiliary spiral (bold gray) and sticky spiral (black) in a representative web of *A. diadematus*. Partial sticky spiral loops (in the web's lower part) are drawn as bold black lines. The cross marks the center of the hub.

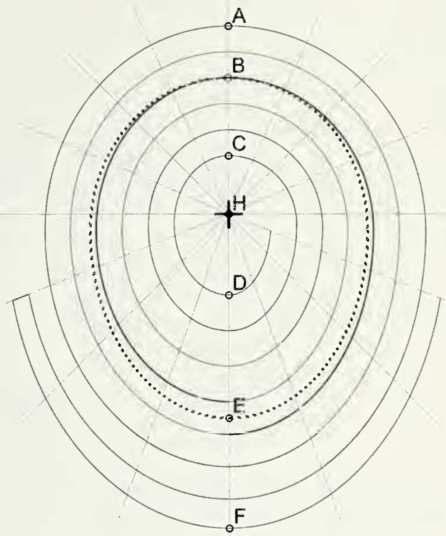

Figure 2.—Schematic drawing of a web to visualize the assessed sticky spiral modifications from round, symmetric webs. The cross marks the center of the hub (H). The sticky spiral is drawn as a fine gray line. The dotted line is the oval corresponding to the sticky spiral loop shown in black; its eccentricity can be calculated as (HB - HE)/(HB + HE). Upper and lower spiral spacing were calculated by dividing the distance between the inner- and outermost sticky spiral loops (AC and DF respectively) by the number of spaces between sticky spiral loops along that radius. Web asymmetry was calculated as (HA - HF)/(HA + HF).

(i.e., loops without a U-turn) of both spirals were converted into a series of ovals of corresponding shape (Fig. 2; Mayer 1952; Zschokke 1993). For all ovals, I calculated the average diameter (width + height)/2 and the vertical eccentricity. As a measure for the vertical eccentricity, I used the ratio (*upper-lower*)/(*upper+lower*), where *upper* was the distance between the hub (H in Fig. 2) and the top of the oval (B), and *lower* was the distance between the hub and the bottom of the oval (E). Spiral loops with the hub in their geometric center thus had an eccentricity of 0.0, and spirals loops with the hub above the center had a negative eccentricity.

For each web, I determined the range of diameters where the two spirals overlap and discarded the ovals outside that range in order to focus on those sticky spiral loops, whose eccentricity is not increased by the partial sticky spiral loops in the lower part of the web (bold lines in Fig. 1; these partial sticky spiral loops are mostly placed outside the auxiliary spiral, Zschokke 1993). From the remaining ovals, the average eccentricity was calculated for both the auxiliary and the sticky spirals, yielding the values auxiliary spiral eccentricity and sticky spiral eccentricity, respectively.

In addition, I counted the number of sticky spiral loops and calculated the average sticky spiral spacing along an entire radius at the top and at the bottom of the web. For these parameters, as well as for the outermost sticky spiral loop, I calculated the asymmetry in the same way as above, [i.e., (upper - lower)/(upper + lower)], yielding the values of sticky spiral ratio, spiral spacing asymmetry, and web asymmetry, respectively. Note that web asymmetry (like hub asymmetry sensu Blackledge & Gillespie 2002) is based on the position of the hub relative to the outermost sticky spiral loop, whereas the similar metric hub displacement (sensu Kuntner et al. 2008) is based on the position of the hub relative to the web frame (Kuntner et al. 2010). Web asymmetry here is used in the same way as in Zschokke (1993) and Coslovsky & Zschokke (2009), whereas Blackledge & Gillespie (2002) used the term web asymmetry index to quantify web shape (deviation of the outermost sticky spiral from a circle). All measures were normally distributed (K-S normality test, $P > 0.75$).

Deviations from 0 of web asymmetry and of the modifications were tested with a one-sample t-Test. The influence of web orientation during auxiliary and sticky spiral building on web asymmetry and on the modifications was tested with 2 factor ANOVAs without interaction. Presented are the Fisher's PLSD post-hoc *P*-values. I calculated these statistics using StatView v. 5.01 for Macintosh.

During web building, spiders can rely on earlier laid threads and on gravity to determine where to place their next thread. In order to determine whether prior existing threads or gravity affect the web modifications, I used the PC (Pure Clusters) algorithm of the program Tetrad (Glymour et al. 2009) to develop a causal model. Causal models can be used to determine causal relationships even when the variables covary, which was the case in the present study.

It is important when developing a causal model that prior knowledge be defined, (i.e., information on which causal relationships are possible, and which are not possible.) In the present case, some causal relationships could be excluded based on the sequence of events since later events cannot influence earlier ones. This prior knowledge is entered by putting the variables into tiers, whereby variables in one tier can only be influenced by variables in the same or in earlier tiers. I placed web orientation during auxiliary spiral building and web orientation during sticky spiral building in the first

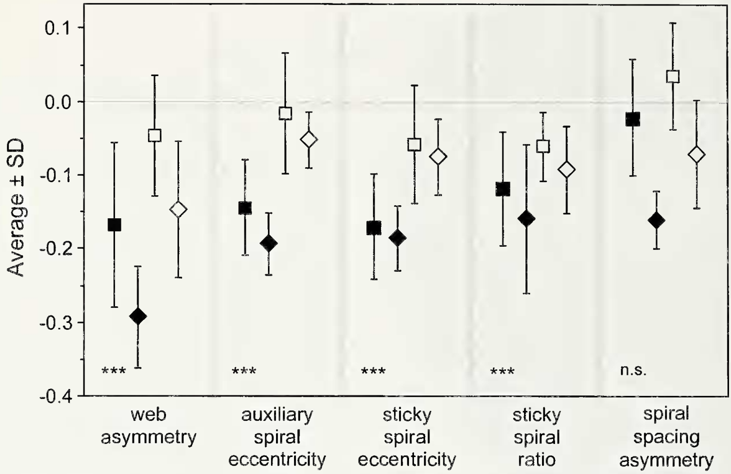

Figure 3.—Average values (± standard deviation) for web asymmetry and for the different web modifications in webs of *A. diadematus*. Solid symbols represent webs that were in a normal (vertical) orientation during auxiliary spiral building. Open symbols represent webs that were in a horizontal orientation. Symbol shape indicates web orientation during sticky spiral building (square = vertical, diamond = horizontal). *** denotes a significant deviation of control webs from zero (one-sample t-Test, $n = 30$, $P < 0.0001$).

tier and defined them as independent of each other. Auxiliary spiral eccentricity was placed in the second tier, and defined as not being influenced by web orientation during sticky spiral building. I placed web asymmetry in the third tier because web asymmetry is defined by the outermost sticky spiral loop, which is placed first. Finally, the remaining variables (sticky spiral eccentricity, sticky spiral ratio, and spiral spacing asymmetry) were placed in the fourth tier. The resulting causal model was then tested with LISREL (Jöreskog & Sörbom 2004) using the maximum likelihood method.

RESULTS

Control webs (i.e., those built entirely in a normal orientation) had an average web asymmetry of −0.167, implying that the hub was placed above the geometric center of the capture area (Fig. 3). Similarly, auxiliary spiral eccentricity, sticky spiral eccentricity, and sticky spiral ratio were all significantly negative. In contrast, spiral spacing asymmetry, while on average negative, did not significantly differ from zero. These results suggest that sticky spiral eccentricity and sticky spiral ratio are the main direct contributors to the observed web asymmetry.

Web asymmetry and all modifications except spiral spacing asymmetry were influenced directly or indirectly by the web orientation during auxiliary spiral building (Table 1). As expected, asymmetries were more pronounced in webs with vertical orientation during auxiliary spiral building (Fig. 3).

The web orientation during sticky spiral building had a significant influence only on spiral spacing asymmetry (Table 1). Interestingly, however, the influence of the orientation during sticky spiral building tended to be opposite to that of the orientation during auxiliary spiral building: a vertical orientation during sticky spiral building tended to reduce web asymmetry and its modifications. This means that the webs with the strongest asymmetry were those in a vertical orientation during auxiliary spiral building and in a horizontal orientation during sticky spiral building.

The PC search algorithm of Tetrad yielded a causal model that suggested that web orientation during auxiliary spiral building influenced auxiliary spiral eccentricity, which in turn influenced sticky spiral eccentricity and web asymmetry. Web asymmetry influenced sticky spiral ratio and both, along with web orientation during sticky spiral building, influenced spiral spacing asymmetry (Fig. 4). The analysis of this causal model with LISREL showed that all these relationships were significant.

DISCUSSION

The results of the present study showed that orb web asymmetry in *A. diadematus* is largely determined during auxiliary spiral building. In particular, web asymmetry and sticky spiral eccentricity were largely determined by auxiliary spiral eccentricity, but were not influenced by gravity during sticky spiral building. These results

Table 1.—Influence of web orientation during auxiliary and sticky spiral building on web asymmetry and the modifications in the web leading to the web asymmetry in *A. diadematus*. Δ = mean difference between webs laid horizontally and webs in the normal (vertical) orientation during auxiliary spiral building and sticky spiral building respectively; *P* values = PLSD post-hoc values from a two-factor ANOVA without interaction.

	Web asymmetry	Auxiliary spiral eccentricity	Sticky spiral eccentricity	Sticky spiral ratio	Spiral spacing asymmetry
Influence of web orientation during auxiliary spiral building	Δ = 0.085 ***P* = 0.0061**	Δ = 0.115 ***P* < 0.0001**	Δ = 0.106 ***P* < 0.0001**	Δ = 0.046 ***P* = 0.0359**	Δ = 0.020 P = 0.3679
Influence of web orientation during sticky spiral building	Δ = −0.057 *P* = 0.0764	Δ = 0.014 *P* = 0.4652	Δ = 0.033 *P* = 0.1237	Δ = −0.010 *P* = 0.6629	Δ = −0.093 ***P* = 0.0002**

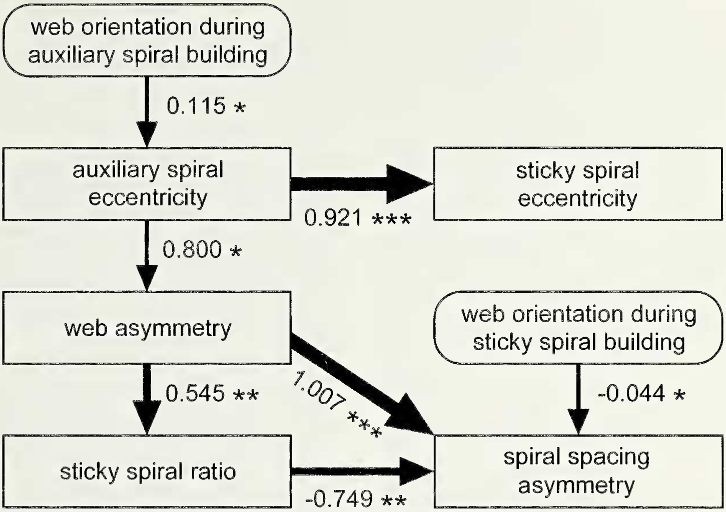

Figure 4.—Relationships between treatments (rounded rectangles) and web modifications leading to web asymmetry in *A. diadematus*. Arrows indicate inferred causalities, numbers indicate linear coefficients, and width of arrows as well as asterisks indicate the strength of the relationship (expressed by *P*-values: * = $P < 10^{-4}$, ** = $P < 10^{-10}$, *** = $P < 10^{-21}$). Model statistics: $df = 13$, $\chi^2 = 103.5$, $P < 0.0001$.

confirm that the auxiliary spiral is used as a guide during sticky spiral building in *A. diadematus* (Witt et al. 1968; Zschokke 1993).

A vertical orientation during sticky spiral building reduced the sticky spiral spacing below the hub. It is possible that such a reduced spiral spacing along the web's lower edge is an adaptation to prevent tumbling prey insects (Eberhard 1989; Zschokke et al. 2006) to fall out of the web since areas with small sticky spiral spacing retain prey better (Blackledge & Zevenbergen 2006). Prey tumbling occurs only in vertical webs; therefore, it makes sense that a vertical web orientation during sticky spiral building induces reduced spiral spacing in the web's lower part.

The web orientation during building of frame and radii was not tested in the present study. Since the hub position relative to the web frame is established during frame building, it is likely that the web orientation at that stage also determines the hub position relative to the frame.

In the present study, gravity was shown to exert a big influence during auxiliary spiral building, whereas its influence during sticky spiral building was limited to spiral spacing asymmetry. Interestingly, earlier studies with the same species gave contrasting results. Webs built during vertical rotation, (i.e., in which the direction of gravity constantly changed during web building) had normal auxiliary spirals, implying that gravity has little influence on auxiliary spiral building. At the same time, these webs had a somewhat to very much disturbed sticky spiral (the degree of disturbance depended on the speed of rotation), suggesting that gravity has a large influence on sticky spiral building (Vollrath 1986, 1988a). Consequently, it is difficult to draw firm conclusions about how the spiders use gravity as an orientation aid during spiral building. All that can be concluded is that the studies by Vollrath and the present study strongly support the hypothesis that the two spirals are built according to different building rules (Vollrath & Mohren 1985; Vollrath 1988b). Furthermore, I suggest that the results of the present study can be used to better analyze the behavioral rules *A. diadematus* follows during spiral building.

To conclude, the results of the present study confirm that in *A. diadematus*, the gravity determines the asymmetry of the auxiliary spiral, that the auxiliary spiral is used as a guide during sticky spiral building and that the spider uses different behavioral rules to build the two spirals. In addition, the present study has shown that the vertical asymmetry of *A. diadematus* webs is achieved by eccentrically placed sticky spiral loops and by partial sticky spiral loops in the lower part of the web, but not by a larger sticky spiral spacing in the lower part of the web.

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